Microhabitat Heterogeneity Promotes Partition of Resources by Syntopic *Peromyscus* in a Midlatitude Temperate Forest

De la Cruz-Arguello Ivan M.[a], *Castro-Campillo Alondra*[a], *Zavala-Hurtado Alejandro*[a], *Salame-Méndez Arturo*[b], *and Ramírez-Pulido José*[a]

[a] *Department of Biology (DB) and* [b] *Department of Reproduction Biology (DBR), Biological and Health Sciences Division (DCBS), Metropolitan Autonomous University-Iztapalapa (UAM-I). AP 55-535- Av. San Rafael Atlixco 186, Vicentina, 09340 Iztapalapa, CDMX, México.*

E-mail of corresponding author: Alondra Castro-Campillo, acc@xanum.uam.mx
Laboratory of Mammals
Edificio "Anexo S" AS-012 PB
Biology, DCBS, UAM-I, AP 55-535
Av. San Rafael Atlixco 186, Vicentina, Iztapalapa
PC 09340, CDMX, México

Abstract

To understand how spatiotemporal changes of microhabitat heterogeneity affect coexistence of syntopic *Peromyscus* within a temperate, mixed forest, along pluvial seasons, we assessed microhabitat zones through multivariate statistics, using onto 23 habitat variables for vertical-horizontal habitat structure. To detect specific microdistribution changes and habitat preferences by the species, we used second order spatial statistics and general linear models. According to their respective morphology and locomotive adaptations, the middle sized, midscansorial *Peromyscus difficilis* was resident all year long and preferred microhabitats with a high log ground cover, while the opportunistic, small sized, cursorial *P. melanotis* changed its occupancy area, depending on density of herbaceous and woody plants cover. Under the more benign microhabitat conditions of rainy season (denser plant coverage, milder temperature), both species showed closer microdistribution patterns; while these became repulsive at the less benign conditions of dry season (scarcer plant cover, colder temperature). Thus, seasonal changes of microhabitat heterogeneity promoted *Peromyscus* coexistence, through dispersion patterns reflecting partition of microhabitat resources.

Key words: Microhabitat selection, Use of space, Small mammals, Dispersion, Resource partition.

Introduction

Spatial heterogeneity has strong impact on coexistence among small mammals, since they become spatially segregated, according to niche preferences such as resource requirements (Valladares *et al*. 2015). Many studies of habitat selection by small mammals have revealed complex relationships between habitat heterogeneity and species coexistence, resource partitioning, and competition among syntopic populations (Monamy and Fox 1999). Consequently, empirical studies have emphasized the significance of structural variation in both biotic and abiotic factors determining animal distributions (M'Closkey and Fieldwick 1975; M'Closkey and Lajoie 1975; Monamy and Fox 1999; Morris 1984; Seagle 1985).

Heterogeneous habitats contain patches of varying size, distribution, resources, environmental conditions, and species composition (Fahrig and Merriam 1994) that vary spatiotemporally, depending on observation scale and habitat type under study (Wiens 2000). It is highly likely that small mammals perceive habitat spatial heterogeneity at fine scale (microhabitat); therefore, both movement and foraging by small mammals are affected by habitat heterogeneity (Bowne *et al.* 1999), having different responses among species or demographic groups within them (Dooley and Bowers 1996). Here we focus on whether small mammals are capable to perceive and to response to microhabitat heterogeneity.

Small mammals use resources selectively, based on their requirements for growth, survival, and reproduction, (Johnson and Gaines 1980). Resource partition by rodents might be due to: a) habitat selection (M'Closkey 1976, 1978); b) optimization of foraging choices (Price and Heinz 1984; Price and Reichman 1987); c) exploitative competition for food in different microhabitats (Price 1978; Bowers 1982), and d) differences in

hoarding behavior (Jenkins and Breck 1998), as well as seed husking (Dayan and Simberloff 1994; Randall 1993). Likewise, predation risk might promote rodents to split resources, such as space, based on occupation of microhabitats where each species is best adapted to compete for resources, while avoiding predators (Kotler *et al*. 1994).

Several studies have quantified variation in resource use at heterogeneous environments, among congeneric and co-family mice species within a community (Kaufman and Kaufman 1989 and references therein). These studies demonstrate resource partitioning by syntopic communities of *Peromyscus* and other genera of rodents, along axes of food availability (Smartt 1978) and space (Barry *et al.* 1990; Galindo and Krebs 1985; Morris 1984). Indeed, syntopic related species are especially valuable in studies of spatial and resource partitioning, since they are most likely to be current or past competitors (Kalcounis-Rüppell and Millar 2002).

Since habitat use varies spatiotemporally (Haim and Rozenfeld 1993) due to distribution and availability of resources, we expect that such variation also affect use of resources and relationships among non-closely related species. Here we analyze how heterogeneity of microhabitats is structured and change through pluvial seasons in a temperate, mixed forest, and how such changes affect coexistence of two syntopic species of *Peromyscus* (*i. e., P. difficilis* and *P. melanotis*), over the following objectives. 1) To assess microhabitats heterogeneity according to vertical and horizontal structure indicators. 2) To analyze spatiotemporal dispersion and availability of microhabitat resources (*e. g.*, space, food in a broad sense, refuges). 3) To determine what kind of spatial relationships occur between both species, depending on seasonal changes in microhabitats heterogeneity (*i.e.*, attraction or positive: sharing of same microhabitats and resources; repulsion or negative: not sharing). 4) To disclose which specific structural elements of the microhabitats better explain abundance in the two *Peromyscus* between

seasons (*i. e.*, partitioning of microhabitat resources).

Material and methods

Ethics statement

Animal capture and handling followed guidelines of the American Society of Mammalogists (Sikes *et al.* 2011). If animals died, corpses were prepared as voucher specimens to house them at the Mammal Collection of the Universidad Autónoma Metropolitana-Iztapalapa (UAMI, Ramírez-Pulido *et al*. 1989). Collecting permit, SEMARNAT-08-049-B, was issued by DGVS, SGPA-09712/13, SEMARNAT, to Alondra Castro-Campillo (ACC).

Study area

Our study area involves a temperate forest of conifers and broad-leaved trees at Parque Nacional Desierto de los Leones (PNDL, CONANP 2006), Mexico City, within the Transmexican Neovolcanic Range. Temperature averages 12.6 ± 6 °C from April to July, while it descends to 8.1 ± 2 °C from December to February. Rainfalls occur from late spring throughout summer (May to August), with an average precipitation of 235 ± 30 mm, though this period can go until mid-fall (October). From winter to early spring (December to March), precipitation mean becomes 12 ± 4 mm, introducing a dry and cold climate. Dominating vegetation by strata include canopy, *Abies religiosa*, *Pinus hartwegii*, *P. leiophylla*, *P. montezumae*, *Prunus serotina*, *Garrya laurifolia*, *Salix paradoxa*, and *Buddleia cordata*; understory shrubs, *Baccharis conferta* and *Senecio* spp.,

and herbs, *Acaena elongata*, *Sigesbeckia jorullensis,* and *Alchemilla procumbens*; ground level, a rich variety of mosses and fungi.

Mice sampling

We captured-recaptured mice along ten months, including the dry and wet seasons (October 2013- August 2014), within a 2,475 m^2 surface plot (Fig. A.1) at 2289 m. The plot was gridded (12 vertical lines, A-L; 10 horizontal lines, 1-10) marking intersections with buried wood stakes (150x2.5x2.5 cm) to construct a coordinate system for independent sampling stations, where we set 120 Sherman live traps (Tallahassee, FL 32303, USA), baited with oat flakes and vanilla scent (Fig. A.1). Traps were set for two nights (2400 trap-nights), shortly before dusk, left open overnight, and checked at next day dawn. To avoid bias in abundance quantification, we code-marked temporally each mouse with gentian violet (De la Cruz-Arguello 2015). We recorded coordinates of any station with a captured mouse, its species (*Peromyscus melanotis*, *P. difficilis*) and its sex by inspection of its external genitalia.

Microhabitat features

To assess environmental spatiotemporal heterogeneity of microhabitat within the entire plot, we delimited an influence zone (sub-plot, Fig. A.1; close-up, Fig. A.1), drawing a rectangle of 2.5 m^2 around each sampling station. We sampled 23 variables (Table 1) in each influence zone during the rainy (June-October) and dry seasons (January-April) to assess components of vertical and horizontal structure of microhabitat, as well as factors affecting distribution of small mammals at fine scales (Morris 1984, 1987; Stapp 1997;

Jorgensen 2004, Coppeto *et al.* 2006; Villanueva-Hernández *et al.* 2017). Table 1 shows assigned ecological meanings for each variable.

We adapted Canfield's (1941) method of Line Intercept (LI) to measure all variables in each pluvial station, for it allows sampling within-plot variation and quantifies changes, both in plant species cover and height over time, by using transects located within a plot. We drew eight graduated transects (cm) from the respective influence zone of each station to cover the 2.5 m^2 sub-plots (Fig. A.1); four 2.5 m transects were cardinally oriented (N, S, E, W), while other four 3.30 m ones were diagonally oriented (NE, NW, SE, SW). Only plants intercepted by diagonal transects were counted for vegetation species richness, number of life forms at different heights (herbaceous and woody plants), and total herbaceous and woody plants; while all transects were used to measure plant coverage at different heights, as well as coverage of fixed elements (*i. e.*, rocks, logs, bare soil, dead organic matter). We calculated coverage percentage of each variable within the sub-plots with the formula $\sum(Xi)\frac{100}{2400}$, where Xi is centimeters occupied by every plant in each transect, and 2400 equals total longitude (sum of the eight transects). We counted directly the number of woody and herbaceous plant life forms at different heights and burrows within each influence zone of every sampling station. We took each hole in the ground ca. 8-12 cm of diameter as a potential burrow for both *Peromyscus* (Álvarez-Castañeda 2005; Fernandez *et al.* 2010).

Statistical data analysis

We standardized all variables and run statistical tests at $p \leq 0.05$ (Zar 1999). To assess microhabitat heterogeneity within the grid, we performed a Hierarchical Cluster Analysis (HCA) in JMP® (ver. 9, SAS Institute Inc., Cary, NC, 1989-2007), using Ward´s method

(1963), where distance between two clusters is the ANOVA' sum of squares between them, added up over all variables. Visual inspection of the dendrogram and of no drastic changes in the variance screeplot, gave us three general groups of stations, which we interpreted as distinct microhabitat types (M1-3). We further statistically validated such microhabitats, as *a priori* groups in Discriminant Analyses (DA, Addinsoft SARL's XLSTAT 2013; F = 9.99 dry; F = 9.64, rains; Wilk's Lambda = 0.0001 in both).

For distribution changes, related to the rainy and dry seasons, on each microhabitat variable, we used Student's *t*-parametric tests in normally distributed microhabitat variables and non-parametric Wilcoxon test for non-normal variables (Table 2), in either one or both seasons. We checked distribution normality of every variable with Kolmogorov-Smirnov tests; there was no multicollinearity among the 23 variables in correlation tests (Zar 1999). In order to know whether the number of stations structuring each type of microhabitat changed between seasons (seasonal microhabitat heterogeneity), we used a contingency table and X^2 test. All these analyses were performed with XLSTAT 13 (Addinsoft SARL).

To examine association between changes in spatial heterogeneity of microhabitats and dispersion patterns of *Peromyscus*, along the entire grid, we conducted a Contingency Tables Analysis. Then, for visualizing associations between the *Peromyscus* and microhabitats, we performed a Correspondence Analysis with the constructed Contingency Tables for both seasons, including abundance of each species in the three microhabitats (Table A.2).

Second order spatial analysis

To map variations in point density captures of small mammals, and to find density gradients across the plot area, we used the Kernel function (PAST, ver. 3.14, Hammer *et al.* 2001). To assess whether both species were associated or disassociated, we compared dispersion patterns between the two mice, using Ripley's K bivariate function (Ripley 1977), since the method considers all distances among individuals located under a Cartesian scheme (X,Y) in a quadrat plot (Ripley 1976, Dale 1999, Zavala-Hurtado *et al*. 2000). A bivariate pattern occurs when there are only two point categories (the two *Peromyscus*); thence, each capture point was assigned to either *P. difficilis* or to *P. melanotis*, beyond its simple location within the grid in Ripley's K bivariate function, $K_{12}(d)$. To evaluate statistical significance of $K_{12}(d)$, we estimated 95 % confidence intervals (95%CI), using a Monte Carlo procedure, based on 1000 random relocation simulations of the sampling stations in the plot (Zavala-Hurtado *et al.* 2000). When L(*d*) was positive and took values over the upper limit of the confidence region, we inferred dissociation or repulsion between the *Peromyscus* at the corresponding (*d*) scale; whereas a significant negative deviation indicated us a pattern of association or attraction between the two mice (Dale 1999). If L(*d*) remains between the limits of the 95%CI for a given value of *d*, the null hypothesis of independence between the two contrasts cannot be rejected (Dale 1999). We used PASSaGE (ver. 2, Rosenberg and Anderson 2011) to carry out Ripley's bivariate K analysis.

Prediction of microhabitat elements affecting use of space by each species

To elucidate what elements of microhabitat structure, directly affected use of space by *Peromyscus difficilis* and *P. melanotis*, we performed General Linear Models (GLIMs), using JMP® (ver. 9, SAS Institute Inc., 1989-2007, Cary, NC,). First, we conducted a Principal Component Analysis (PCA) onto the means of the 23 variables to obtain functions summarizing the greatest variance at each season. Thenceforth, we only used functions explaining > 10 % of variance, as independent variables to predict likelihood that a mouse of *P. difficilis* or *P. melanotis* could be present in each of the sampling stations, either in dry or rainy seasons, within the GLIMs. In each model, response variable was capture frequency of both species in each station of the plot, and we assumed a Poisson distribution with a log link function. Criteria for selecting models that most explained number of mice for each species at each season in the sampling stations, included: model significance of $p > 0.05$; lowest Akaike Information Criterion (AIC), *i. e.*, measure of variance explained by the model (Posada and Buckley 2004); and its deviation (Deviance); as well as biological and ecological meaning of results.

Results

Behavior of 23 variables of microhabitat between seasons

Sixteen variables from the microhabitat structure showed statistical differences in their mean values (Table 2) between pluvial seasons, main changes occurring in variables that represented herbaceous vegetation, according to plant coverage at different heights, and vegetation species richness (VSR). As expected in overall, woody life forms were more

stable between seasons (Table 2). Components of microhabitat showing no statistical change between seasons were frequency of 10 cm height herbaceous plants (FH11), frequency of both 35 cm (FW23) and 50 cm (FW24) woody plants, as well as coverage of logs (CLO), rocks (RC), and bare soil (BS). Therefore, space configuration given by these structural features remained stable in both seasons.

Microhabitat heterogeneity

The dendrogram from cluster analysis revealed three different kinds of microhabitats (M1, M2, and M3) within the sampling plot in each season. M1 included more sampling stations during the dry season, while M2 covered the majority of sampling stations during the rainy season (Table A.3). Indeed, Fisher's exact test of Contingency Tables Analysis revealed significant changes in number of sampling stations ($p > 0.004$) from dry to rainy seasons with main changes occurring between M1 ($X^{2 =}$ 2.123, $0.05 > p$) and M2 ($X^{2 =}$ 3.348, $0.05 > p$), especially in the latter, since it augmented 24 sampling stations from the dry season to the rainy season. Conversely, number of sampling stations remained quite stable in M3 ($X^2 = 0.011$) throughout the study (Table A.3).

Discriminant analyses validated heterogeneity of the three microhabitats (Fig. 1) within and between pluvial seasons. Differences in apportion of variance percentages in the discriminant functions was more clear during the rainy season (dry season: F1 = 58.67 %, F2 = 42.32 %; rainy season: F1 = 72.581 %, F2 = 27.419 %) (Fig. 1). Discriminant functions explained variation due to woody plants in the understory in the dry season, while herbaceous vegetation together with decayed matter and logs became more relevant at rains. Wilk's Lambda showed that at least one microhabitat mean differed statistically from the others in both dry ($p > 0.0001$) and wet ($p > 0.0001$) seasons (Fig. 1). These

results corroborated spatial heterogeneity drawn from cluster analysis of individual station features in the grid plot. During the dry season, 93.33 % of individual sampling stations remained correctly classified, and 94.17 % of them during the rainy season (Table A.3, Fig. 1).

Description of microhabitats within the plot

Microhabitat 1. M1 (Fig. 1) was characterized by low amounts, or even absence, of vegetation cover at different heights (VC) and low frequency of herbaceous and woody plants (FH and FW, respectively) in the understory. In contrast, organic matter on the ground (OM) was the most frequent component. This microhabitat was also distinctive for having a large coverage of logs (CLO) on the ground and for being the microhabitat with the major presence of burrows (BW).

Microhabitat 2. M2 (Fig. 1) was the largest area covered by herbaceous life forms at different heights; vegetation species richness (VSR) and total number of herbaceous plants (TH) remained also very high. Woody life forms at 25 cm (FW22) were present but at low frequencies, while FW24 and FW25 remained at higher frequencies. Coverage on the ground of small logs or dead wood (CLO), of rocks (RC), and organic matter (OM) were very low during the study. Bare soil surface (BS) increased to higher amounts during the dry season, while it decreased at the rainy season. There were no burrows (BW) in this microhabitat.

Microhabitat 3. In M3 (Fig. 1), VC25, VC35, VC50, and VC100 showed high values, while vegetation species richness (VSR) averaged the highest compared to other microhabitats. Total number of woody plants (TW) and frequency of woody plants at different heights (FW21-25) remained very high, while total number of herbaceous plants

(TH) was very low. Vegetation coverage at 10 cm (VC10), rocks (RC), logs (CLO), and bare soil surface (BS) were very low during the dry season; however, VC10 increased in the rainy season. Conversely, OM was present in the dry season, but decreased in the rainy season. Number of burrows (BW) remained quite scarce.

Association between the microhabitats and species

Kernel Graphs (Fig. 2) indicated that the two species used space distinctively, since they were differentially scattered along the plot. *Peromyscus difficilis* was more abundant during the dry season, occupying a large portion of the plot. Instead, *P. melanotis* increased its abundance during the rains when it seemed to displace *P. difficilis* into other sampling stations (Fig. 2). Distribution rearrangements between seasons implied that one species occupied some stations more frequently than the other, and vice versa (Fig. 2). Indeed, the two X^2 tests yielded statistical abundance differences in each species at both microhabitats and seasons (Table A.2: dry season; R^2 (U) = 0.09, n = 111, df = 2, Likelihood Ratio X^2 = 15.07, p = 0.00005; rainy season; R^2 (U) = 0.02, n = 168, df = 2, Likelihood Ratio X^2 = 6.40, p = 0.0406).

During dry season (Fig. 3a and Table A.2), *Peromyscus difficilis* was highly associated to M2 (80 % captured mice) and frequently associated to M1 (64 % captured mice); conversely, *P. melanotis* showed frequent association to M3 (66 % captured mice). Spatial use of microhabitats changed for both species in the rains (Fig. 3b, and Table A.2), showing again a microhabitat partition, though less obvious: in the Correspondence Analysis, 61 % of captured *P. difficilis* occurred in M1 and this species was also associated to M3, while 60% captured mice of *P. melanotis* was associated to M2.

Spatial Patterns of attraction or repulsion between species

During the dry season, Ripley's bivariate K showed a statistical significant pattern of repulsion for both *Peromyscus* in all analyzed distances of the entire plot (Fig. 4a). Such repulsion pattern turned over in almost all distances during the rainy season (Fig. 4b), since the two species became more associated, sharing microhabitats in almost all capture stations. However, in the rainy season statistical significant peaks of repulsion reappeared between the species at distances of five, ten, and 14 m (Fig. 4b). Analyses also revealed intensity of these patterns; e.g., likelihood for finding individuals of *P. difficilis* and *P. melanotis* together at the same capture station was very low during the dry season (Fig. 4a), while this probability increased in the rainy season (Fig. 4b).

Structural components of microhabitats affecting distribution of small mammals

In the dry season, Generalized Linear Model (GLIM) of the effect of PC1 and PC3 from the PCA on abundance of *P. difficilis* (Fig. A.2), resulted statistically significant; indeed with a positive relationship (AICc 212.55). Environmental variables with higher scores in the PC1 (p = 0.0186) were total number of herbaceous plants (TH), vegetation species richness (VR), and vegetation cover at 10 cm height (VC10). In PC3 (p = 0.0001), characterizing variables were number of logs on the ground (CLO), as well as presence of burrows (BW). These five variables were also the main elements characterizing M2 (PC1) and M3 (PC3), the two microhabitats to which *P. difficilis* was associated in this season. As for *P. melanotis* (Fig. A.3), the GLIM model showed it was only positively associated to PC2 (AICc = 204.47, p = 0.0001). Here, among the four variables with higher scores, were total number of woody vegetation (TW) and frequency of woody life forms at 10 cm height (FW21), the two main elements at M3 for the dry season

During the rainy season, a similar pattern of microhabitat partition occurred between the two species. *P. difficilis* (Fig. A.2) was now mainly associated (AICc = 281.77) to total number of woody plants (TW), and vegetation cover at 10 cm of height (VC10), in PC2 (p = 0.0065); to number of logs on the ground (CLO), in PC3 (p = 0.0210); and to vegetation cover at 50 cm and 100 cm (VC50, VC100), in PC4 (p = 0.0076). The latter involved variables with high presence at M1 and M3 during the wet season, where more *P. difficilis* occurred. On the other hand, *P. melanotis* (Fig. A.2) was only associated to PC1 (AICc = 246.46, p = 0.0262), increasing as the number of total herbaceous plants (TH), vegetation richness (VR), and the plant cover at all analyzed heights (VC10-100 cm) also increased. Thence, PC1 represented variables commonly found in greater amounts at M2, the microhabitat with more abundance of *P. melanotis.* Therefore, both results of Contingency Tables Analysis, Correspondence Analysis, and GLIMs models showed that the two syntopic species of *Peromyscus* switched and split resources in space, as environmental conditions changed (Fig. A.2).

Discussion

Our findings on microhabitat associations of rodents in a patch of a mid-latitude temperate forest, concur with the habitat heterogeneity coexistence hypothesis (Cramer and Willig 2002; Valladares *et al.* 2015). We found that both *Peromyscus* were sensitive to slight modifications of habitat structure and that the three microhabitats provided different resources for each one. Our results also suggest that coexistence between these syntopic *Peromyscus* is mainly facilitated by temporal differences in space structure, and probably also by changes on availability of both food and shelter that go with it (Pianka 1973; Schoener 1974). For instance, *P. difficilis* was more associated to M1 and M2 by

the dry season, while *P. melanotis* was highly associated to M3. Conversely, *P. difficilis* was more associated to M1 and slightly associated to M3 by the rainy season, while *P. melanotis* was highly attracted to M2. Partition in space use has already been documented for coexisting species of *Peromyscus* within a community; *i.e.*, extensive studies of niche partitioning by *Peromyscus leucopus* and *P. maniculatus* (Kaufman and Kaufman 1989). Moreover, several studies have demonstrated variation in spatial resource use by congeneric species (Barry *et al.* 1990; Dooley and Dueser 1996; Kalcounis-Rüppell and Millar 2002).

In our study, *P. difficilis* remained associated to M1 and M3 in both seasons, especially to the former during the wet season. Number of fallen logs was very high at M1, while understory complexity, together with woody vegetation, were more relevant in M3. Such microhabitats represent small patches of food for small mammals, offering invertebrates (Bellows *et al*. 2001), flowers, grains, and fungi items (Bowman *et al.* 2001). In these microhabitats, individuals of *P. difficilis* can also use fallen logs as shelter, as well as pathways for quick and straight locomotion inside the forest (Bellows *et al.* 2001; Dewalt *et al.* 2003). Indeed, fallen logs promote structural complexity of forests and may enhance positive interaction among species of small mammals (Bowman and Facelli 2013). GLIM's analyses showed that abundance of *P. difficilis* was explained by PC1 and PC3 during the dry season and by PC2-4 in the rainy season. In the dry season, variables contributing most to PCA ordination in PC1 and PC3 were total number of herbaceous vegetation (TH) and number of logs on the ground (CLO), as well as burrows (BW). While in the dry season, PC2-4 represented woody vegetation (TW), number of logs, burrows, and understory complexity (VR). Bellows *et al*. (2001) found a similar result in a high latitude temperate forest (Virginia, USA), where distribution of a small mammal, generalist species was associated with the diameter of fallen logs, frequency of

shrubs, and degree of canopy closure. Association between rodents and fallen logs was also documented for *Nectomys squamipes* that builds up its nests inside decomposed, fallen logs (Briani *et al.* 2004); this has also been recorded for other rodent species in several biomes with different vegetation types (*e. g.*, *Rattus rattus*, *Nesomys audeberti* in Lehtonen *et al.* 2001; *Oligoryzomys nigripes* in Dalmagro and Vieira 2005).

In contrast, *P. melanotis* showed a close association with only one PC over each pluvial season. During the dry season, abundance of this species was only associated to PC2, which represented total number of woody vegetation (TW). Then by the rainy season, the species became only related to PC1, which accounted for understory complexity dominated by herbaceous life forms (TH). Association between abundance of rodents and habitats with increased understory density, has been interpreted as protection against aerial predators (Dalmagro and Vieira 2005), or as preference for more complex habitats that enable for vertical stratifications and, thus for extended coexistence inside fragments (Grelle 2003; Johnson 2007).

Coexistence of both *Peromyscus* at the study plot, must be also related to its intrinsic factors. For instance, partition of space by these syntopic deermice must be facilitated by their respective locomotive habits as semiarboreal (*P. difficilis*) and cursorial (*P. melanotis*). Both the long tail and wide sole surface of *P. difficilis*, must enable it to rush and climb along shrubs or trees (Álvarez-Castañeda 2005), thus easing its preference for habitats where it can escape from predators. Indeed, adult color coat changed in *P. difficili*s between pluvial seasons, becoming more similar to ground litter; *e. g.*, in this resident deermouse, color phenotype plasticity must be a cryptic response elicited against predators. On the other hand, a smaller sized body, together with a shorter tail and narrower soles (Fernandez *et al.* 2010), should enable the cursorial *P. melanotis* to occupy such zones as M2 and M3, where it cannot be easily spotted by predators

through a dense vegetation cover, so it can scape very quickly. Indeed, high shrubs cover provide both protection from predators and food sources, since seeds may be concentrated under shrub canopies (Thompson 1982; Mohammadi 2010). In fact, rodents usually avoid foraging in unsheltered microhabitats and forest edges where they are more likely to be spotted by avian (Kotler *et al.* 1991) and other vertebrate predators (Morris and Davidson 2000; Mohammadi 2010). *P. melanotis* generally showed a more opportunistic pattern of habitat occupation as compared to the larger sized *P. diffiilis*. Chupp (2002) also showed an opportunistic habitat by small sized *Peromyscus leucopus*, which he related to predation risk. Further studies about influence of predation on opportunistic behavior of *P. melanotis* are needed.

One possible consequence of such extrinsic and intrinsic operating factors is that *P. difficilis* remained more abundant and always present at the microhabitats with more stable elements in the study area (our unpublished data), while *P. melanotis* only increased its abundance during the rainy season, when environmental conditions became more benign and plant cover became denser. Since rains promote increase of primary productivity, allowing more resource availability (mainly food) and enhancing microhabitat carrying capacity, such habitat changes facilitate coexistence between both *Peromyscus*, and with other small land mammals in the area (Castro-Campillo *et al*. 2008, 2012). Ripley's bivariate K supported and shed light into such outcome, since the species showed repulsion between them in all analyzed distances during the dry season; *i.e.*, it was almost null that a mixed pair used the same space or microhabitat during this season. Conversely, intensity of such repulsion decreased substantially during the rainy season; moreover, at some analyzed distances, the two deermice showed an association pattern. Our results also indicate that in these two syntopic *Peromyscus*, both microhabitat use and spatial organization are seasonally variable (Brown and Zeng 1989; Cramer and

Willig 2002).

Finally, we want to highlight and recommend our sampling of environmental features and quantitative analyses, especially for Ripley's bivariate K, as neither one has been extensively used in studies focusing on the spatial dynamics of dispersion in small rodents, despite its helpful advantages. The methodological approach used here, together with the gathered evidences became relevant for providing us with basic information about the ability of this two *Peromyscus* to split resources in a mid-latitude temperate forest at the edge of a megalopolis, which continuous enlargement produces fragmentation and patching of natural microhabitats. Therefore, our local scope was explicitly designed at this initial point, to focus on small sized rodents with low vagility. Besides, we successfully aimed to reconstruct vegetation structure, in order to provide us with clues as how to eventually manage such perturbed ecosystems for conservation purposes. We also think that our methodology can be helpful in other scenarios for understanding small rodents, such as ethological dynamics, activity patterns, and reproductive systems at either or both intra or interpopulation levels.

Acknowledgments

We thank Juan Luis Patiño Ortega and Claudia Peralta Juarez for their fieldwork assistance and friendly logistic support. The staff at UAMI mammal scientific collection, kindly provided all the facilities for specimen curation and housing. Authorities in charge of DLNP (CORENA, SEMARNAT), as well as the forest rangers and administration staff at the National Park buoyed us with information, security, and logistics to complete our studies. This paper contains partial information from the thesis of Master in Biology (DCBS, UAM-I) of IMDA; IMDA received financial support through a fellowship

(283799, CVU 479479) from the National Council of Science and Technology (CONACyT). This study was supported by annual grants (143.***.46 IB-DCBS-UAMI, 2013-2017) to AACC.

References

Álvarez-Castañeda, S.T. (2005). *Peromyscus melanotis*. Mamm. Spec. 764, 1-4.

Barry Jr, R.E., Heft, A.A., Baummer, TE. (1990). Spatial relationships of syntopic white-footed mice, *Peromyscus leucopus*, deer mice, *Peromyscus maniculatus*, and red-backed voles, *Clethrionomys gapperi*. Can Field-Nat. 104, 87-393.

Bellows, A.S., Pagels, J.F., Mitchell, J.C. (2001). Macrohabitat and microhabitat affinities of small mammals in a fragmented landscape on the upper coastal plain of Virginia. Amer. Midl. Nat. 146(2), 345-360.

Briani, D.C., Palma, A.R., Vieira, E.M., Henriques, R.P. (2004). Post-fire succession of small mammals in the Cerrado of central Brazil. Biodivers. Conserv. 13(5), 1023-1037.

Brown J.H, Zeng, Z. (1989). Comparative population ecology of eleven species of rodents in the Chihuahuan Desert. Ecol. 70(5), 1507-1525.

Bowers, M.A. (1982). Foraging behavior of heteromyid rodents: field evidence of resource partitioning. J. Mamm. 63(3), 361-367.

Bowers, J.H., Baker, RJ., Smith, M.H. (1973). Chromosomal, electrophoretic, and breeding studies of selected populations of deer mice (*Peromyscus maniculatus*) and black-eared mice (*P. melanotis*). Evol. 27(3), 378-386.

Bowman, J., Forbes, G., Dilworth, T. (2001). Landscape context and small-mammal abundance in a managed forest. For. Ecol. Manag. 140(2), 249-255.

Bowman, A.S., Facelli, J.M. (2013). Fallen logs as sources of patchiness in chenopod shrublands of South Australia. J. Arid Environ. 97, 66-72.

Bowne, D.R., Peles, J.D., Barrett, GW. (1999). Effects of landscape spatial structure on movement patterns of the hispid cotton rat (*Sigmodon hispidus*). Landsc. Ecol. 14(1), 53-65.

Canfield, R.H. (1941). Application of the line interception method in sampling range vegetation. J. For. 39(4), 388-394.

Carey, A.B., Harrington, C.A. (2001). Small mammals in young forests: implications for management for sustainability. For. Ecol. Manag. 154(1), 289-309.

Carleton, M.D. (1989). Systematic and evolution. pp. 7-141 in Advances in the study of *Peromyscus* (Rodentia) (G. L. Kirkland, Jr., and J. N. Layne, eds.). Texas Tech University, Lubbock.

Castro-Campillo, A., León-Altamirano, L., Herrera-Muñoz, J., Salgado-Ugarte, I., Mendieta Márquez, E., Contreras-Montiel, JL., Serrano, H., Ramírez-Pulido, J., Salame-Méndez, A. (2012). Is there difference between T contents in two populations of the Black eared Mouse, living under similar conditions but with differences in two population patterns? Acta Zool. Mex. (n. s.) 28(3), 525-539.

Castro-Campillo, A., Salame-Méndez, A., Vergara-Huerta, A., Castillo, A., Ramírez-Pulido, J. (2008). Fluctuaciones de micromamíferos terrestres en bosques templados aledaños a la ciudad de México. Distrito Federal. Pp. 391-410 in Avances en el Estudio de los Mamíferos de México (Lorenzo, C, Espinoza E, Ortega J, eds.).

Publicaciones especiales. Vol. II, Asociación Mexicana de Mastozoología, A. C., México, D. F. 726 pp.
Cramer, M.J., Willig, M.R. (2002). Habitat heterogeneity, habitat associations, and rodent species diversity in a sand–shinnery-oak landscape. J. Mamm. 83(3), 743-753.
Coppeto, S.A., Kelt, D.A., Van Vuren, D.H., Wilson, J.A., Bigelow, S. (2006). Habitat associations of small mammals at two spatial scales in the northern Sierra Nevada. J. Mamm. 87, 402-413.
Chupp, AD. (2002). Habitat selection in four sympatric small mammal species and the effects of potential predators on *Peromyscus leucopus*. Master of Science Thesis. Department of Biology, Ohio University, 61 pp.
Dale, MRT. (1999). Spatial pattern analysis in plant ecology. Cambridge University Press.
Dalmagro, A.D., Vieira, E.M. 2005. Patterns of habitat utilization of small rodents in an area of Araucaria forest in Southern Brazil. Austral Ecol. 30, 353-362.
Dayan, T., Simberloff, D. (1994). Morphological relationships among coexisting heteromyids: an incisive dental character. Amer. Nat. 143(3), 462-477.
De la Cruz-Argüello, I.M. (2015). Patrones de microdistribución en los mamíferos pequeños en vegetación secundaria en el Parque Nacional Desierto de los Leones. Tesis de Maestría en Ciencias. División de Ciencias Biológicas y de la Salud, Universidad Autónoma Metropolitana, Unidad Iztapalapa, pp. 256.
DeWalt, S.J., Maliakal, S.K., Denslow, J.S. (2003). Changes in vegetation structure and composition along a tropical forest chronosequence: implications for wildlife. For. Ecol. Manag. 182(1), 139-151.
Dooley, J.L., Dueser, R.D. (1996). Experimental tests of nest site competition in two *Peromyscus* species. Oecologia 105, 81-86
Dooley, J.L., Bowers, M.A. (1998). Demographic responses to habitat fragmentation: experimental tests at the landscape and patch scale. Ecol. 79(3), 969-980.
Fahrig, L., Merriam, G. (1994). Conservation of fragmented populations. Conserv. Biol. 8(1), 50-59.
Fernández, J.A., García-Campusano, F., Hafner, M.S. (2010). *Peromyscus difficilis* (Rodentia: Cricetidae). Mamm. Spec. 42(1), 220-229.
Forsman, E.D., Meslow, E.C., Wight, H.M. (1984). Distribution and biology of the spotted owl in Oregon, USA. Wildl. Monogrsaphs. 87, 1-64.
Galindo, C., Krebs, C.J. (1985). Habitat use and abundance of Deer Mice: interactions with Meadow Voles and Red-backed Voles. Can. J. Zool. 63, 1870-1879.
Gunther, P.M., Horn, B.S., Babb, G.D. (1983). Small mammal populations and food selection in relation to timber harvest practices in the western Cascade Mountains. Northwest Sci. 57, 32-44.
Grelle, C.E.V. (2003). Forest structure and vertical stratification of small mammals in a secondary Atlantic forest, southeastern Brazil. Stud. Neotrop. Fauna Environ. 38(2), 81-85.
Haim, A., Rozenfeld, F.M. (1993). Temporal segregation in coexisting *Acomys* species: the role of odour. Physiol. Behav. 54(6), 1159-1161.
Hammer, Ø., Harper, D.A.T., Ryan, P.D. (2001). PAST: PAleontological STatistics software package for education and data analysis. Palaeontol. Electronica 4, 1-9.
Jenkins, S.H., Breck, S.W. (1998). Differences in food hoarding among six species of heteromyid rodents. J. Mamm. 79(4), 1221-1233.
Johnson, M.L., Gaines, M.S. (1990). Evolution of dispersal: theoretical models and empirical tests using birds and mammals. Annu. Rev. Ecol. Syst. 21(1), 449-480.
Johnson, M.D. (2007). Measuring habitat quality: a review. Condor 109(3), 89-504.

Jorgensen, E.E. (2004). Small mammals use of microhabitat reviewed. J. Mamm. 85(3), 531-539.

Kalcounis-Rüppell, M.C., Millar, J.S. (2002). Partitioning of space, food, and time by syntopic *Peromyscus boylii* and *P. californicus*. J. Mamm. 83, 614-625.

Kaufman, D.W., Kaufman, G.A. (1989). Population biology. pp. 233-271 *in* Advances in the study of *Peromyscus* (Rodentia) (G. Kirkland, JR. and J. Layne, eds.). Texas Tech University Press, Lubbock.

Kotler, B.P., Ayal, Y., Subach, A. (1994). Effects of predatory risk and resource renewal on the timing of foraging activity in a gerbil community. Oecologia 100(4), 391-396.

Kotler, B.P., Brown, J.S., Hasson, O. 1991. Factors affecting gerbil foraging behavior and rates of owl predation. Ecol. 72, 2249-2260.

Lehtonen, J.T., Mustonen, O., Ramiarinjanahary, H., Niemelä, J., Rita, H. (2001). Habitat use by endemic and introduced rodents along a gradient of forest disturbance in Madagascar. Biodivers. Conserv. 10, 1185-1202.

Maser, C., Maser, Z. (1988). Interactions among squirrels, mycorrhizal fungi, and coniferous forests in Oregon. Great Basin Nat. 48, 358-369.

M'Closkey, R.T., Fieldwick, B. (1975). Ecological separation of sympatric rodents (*Peromyscus* and *Microtus*). J. Mamm. 56(1), 119-129.

M'Closkey, R.T., Lajoie, D.T. (1975). Determinants of local distribution and abundance in White-Footed Mice. Ecol. 56(2), 467-472.

M'Closkey, R.T. (1976). Community structure in sympatric rodents. Ecol. 57(4), 728-739.

M'Closkey, R.T. (1978). Niche separation and assembly in four species of Sonoran Desert rodents. Amer. Nat. 112(986), 683-694.

Mohammadi, S. (2010). Microhabitat selection by small mammals. Adv. Biol. Res. 4(5), 283-287.

Monamy, V., Fox, B.J. (1999). Habitat selection by female swamp rats (*Rattus lutreolus*) drives asymmetric competition and coexistence with long-tailed mice (*Pseudomys higginsi*). J. Mamm. 80, 232-242.

Morris, D.W. (1987). Ecological scale and habitat use. Ecol. 68(2), 362-369.

Morris, D.W. (1984a). Sexual differences in habitat use by small mammals: evolutionary strategy or reproductive constraint? Oecologia 65(1), 51-57.

Morris, D.W. (1984b). Patterns and scale of habitat use in two temperate-zone, small mammal faunas. Can. J. Zool. 62(8), 1540-1547.

Pianka, E.R. (1973). The structure of lizard communities. Annu. Rev. Ecol. Syst. 4(1), 53-74.

Price, M.V., Heinz, K.M. (1984). Effects of body size, seed density, and soil characteristics on rates of seed harvest by heteromyid rodents. Oecologia 61(3), 420-425.

Price, M.V., Reichman, O.J. (1987). Distribution of seeds in Sonoran Desert soils: implications for heteromyid rodent foraging. Ecol. 68(6), 1797-1811.

Price, M.V. (1978). The role of microhabitat in structuring desert rodent communities. Ecol. 59(5), 910-921.

Pyare, S., Longland, W.S. (2001). Patterns of ectomycorrhizal fungi consumption by small mammals in remnant old-growth forests of the Sierra Nevada. J. Mamm. 82, 681-689.

Ramírez-Pulido, J., Lira, I., Gaona, S., Müdespacher, C., Castro-Campillo, A. (1989). Manejo y mantenimiento de colecciones mastozoológicas. Universidad Autónoma Metropolitana, Unidad Iztapalapa, México, D.F.

Randall, J.A. (1993). Behavioural adaptations of desert rodents (Heteromyidae). Anim. Behav. 45(2), 263-287.

Ripley, B.D. (1976). The second-order analysis of stationary point processes. J. Appl. Probab. 13(2), 255-266.

Rosenberg, M.S., Anderson, C.D. (2011). PASSaGE: pattern analysis, spatial statistics and geographic exegesis. Version 2. Methods Ecol. Evol. 2(3), 229-232.

Schoener, T.W. (1974). Resource partitioning in ecological communities. Science 185(4145), 27-39.

Seagle, S.W. (1985). Patterns of small mammal microhabitat utilization in cedar glade and deciduous forest habitats. J. Mamm. 66(1), 22-35.

Smartt, R.A. (1978). A comparison of ecological and morphological overlap in a *Peromyscus* community. Ecol., 59:21.

Thompson, S.D. (1982). Structure and species composition of desert heteromyid rodent species assemblages: effects of a simple habitat manipulation. Ecol. 63(5),1313-1321.

Valladares, F., Bastias, C.C., Godoy, O., Granda, E., Escudero, A. (2015). Species coexistence in a changing world. Front. Plant Sci. 6, art. 866.

Vander Wall, S.B., Thayer, T.C., Hogbe, S.B., Beck, M.J., Roth, J.K. (2001). Scatter-hoarding behavior of deer mice (*Peromyscus maniculatus*). West. N. Am. Nat. 61, 109-113.

Villanueva-Hernández, A.I., Delgado-Zamora, D.A., Heynes-Silerio, S.A., Ruacho-González, L., López-González, C. (2017). Habitat selection by rodents at the transition between the Sierra Madre Occidental and the Mexican Plateau, México. J. Mamm. 98(1), 293-301.

Ward, J.H. (1963). Hierarchical grouping to optimize an objective function. J. Am. Stat. Assoc. 58(301), 236-244.

Wiens, J.A. (2000). Ecological heterogeneity: an ontogeny of concepts and approaches. *In*: The Ecological Consequences of Environmental Heterogeneity (Stewart AJA, John EA, Hutchings MJ, eds). Blackwell, Oxford, Pp. 9-31.

Zar, JH. (1999). Biostatistical Analysis. Prentice Hall, Princeton.

Zavala-Hurtado, JA., Valverde, PL., Herrera-Fuentes, MC., Diáz-Solis, A. (2000). Influence of leaf-cutting ants (*Atta mexicana*) on performance and dispersion patterns of perennial desert shrubs in an inter-tropical region of Central Mexico. J. Arid Environ. 46, 93-102.

Zielinski, W.J., Spencer, W.D., Barrett, R.H. (1983). Relationship between food habits and activity patterns of Pine Martens. J. Mamm. 64, 387-396.

Table 1. Environmental variables used to measure horizontal and vertical structure of microhabitat at each sampling station, showing its ecological interpretation (kind or resource type) for both species of *Peromyscus*.

Variable code	Structure	Predation		Resources				
	Spatial heterogeneity	Diminished risk	Refuges	Breeding Space	Food	Temporal food and refuges	Permanent	Resting places
			Vegetation Cover (cm)					
VC10	X	X			X	X		X
VC25	X	X		X	X	X		X
VC35	X	X		X	X	X		X
VC50	X	X		X	X	X		X
VC100	X	X		X	X	X		X
			Frequency of Herbaceous Plants (cm)*					
FH11	X	X		X	X	X		X
FH12	X	X		X	X	X		X
FH13	X	X		X	X	X		X
FH14	X	X		X	X	X		X
FH15	X	X		X	X	X		X
			Frequency of Woody Plants (cm)*					
FW21	X	X	X	X	X	X	X	X
FW22	X	X	X	X	X	X	X	X
FW23	X	X	X	X	X	X	X	X
FW24	X	X	X	X	X	X	X	X
FW25	X	X	X	X	X	X	X	X
			Vegetation Species Richness					
VR	X	X	X	X	X	X	X	X
			Total Herbaceous Plants					
TH	X	X		X	X	X		X
			Total Woody Plants					
TW	X	X	X	X	X	X	X	X
			Rock Coverage					
RC	X	X	X	X			X	X
			Organic Matter (litter, twigs, small trunks)					
OM	X				X	X		
			Bare Soil					
BS	X					X		
			Coverage of Logs (stumps, fallen trunks)					
CLO	X	X	X	X			X	X
			Number of Burrows					
BW	X	X	X	X			X	X

* = Frequencies of plant types (FH, FW) involve the same heights as in VC.

Table 2. Normality (**NOR**) tests for 22 variables (**VAR**) of microhabitat, and comparisons[abc] (**COM**) for average values between the dry (**DRY**) and rainy (**RAINS**) seasons, respectively. Variable names in Table 1.

VAR	NOR[a]		COM	VAR	NOR[a]		COM	VAR	NOR[a]		COM
	DRY	RAINS			DRY	RAINS			DRY	RAINS	
BS	0.0001	0.0001	*1.0*[c]	**VC100**	0.002	0.003	0.0001[c]	**TW**	*0.143*	*0.08*	0.0004[b]
CLO	0.0001	0.0001	*0.972*[c]	**VR**	0.006	*0.082*	0.0001[b]	**FW21**	0.0001	0.0001	0.004[c]
OM	0.010	0.034	0.0001[c]	**TH**	0.0001	*0.072*	0.0001[b]	**FW22**	0.0001	0.0001	0.026[c]
RC	0.0001	0.0001	*0.432*[c]	**FV11**	0.015	0.028	*0.658*[c]	**FW23**	0.0001	0.0001	*0.875*[a]
VC10	0.002	0.041	0.0001[c]	**FV12**	0.0001	0.0001	0.001[c]	**FW24**	0.0001	0.0001	*0.378*[c]
VC25	0.009	0.003	0.0001[c]	**FV13**	0.0001	0.0001	0.0001[c]	**FW25**	0.0001	0.001	0.0001[c]
VC35	0.0001	0.002	0.0001[c]	**FV14**	0.0001	0.0001	0.0001[c]				
VC50	0.0001	0.019	0.0001[c]	**FV15**	0.0001	0.0001	0.0001[a]				

Parametric: [a]Kolmogorov-Smirnov; [b]Student for two samples; non-parametric: [c]Wilcoxon). The *p*-values in italics do not reject normality ($p \geq 0.05$), or do not indicate significant differences between pluvial seasons.

Figure legends

Fig. 1. Classification of the three types of microhabitats (M1 = red, M2 = green, M3 = blue), in the dry (a) and rainy (b) seasons, respectively, resulting from the behavior and the distributions of the 23 structural variables. Below each figure is observed the classification by Discriminant analysis made with the *a priori* classification of the cluster analysis.

Fig. 2. Spatial analysis with Kernel density points showing capture frequencies for *P. difficilis* at dry (a) and rainy (b) seasons, and for *P. melanotis* at dry (c) dry and rainy (d). Dots depict actual capture points, while darker shadowing indicates higher density.

Fig. 3. Correspondence analysis from contingency tables of frequency capture data for each deermouse (*P. difficilis* and *P. melanotis*) in each microhabitat (M1-3), during the dry (a) and rainy (b) seasons, respectively. Axis c1 and c2 indicate the coordinates resulted from the ordination of each variable from the analysis.

Fig. 4. Ripley's bivariate K Analysis for interactions between the two *Peromyscus*. (a) Repulsion between both species in all analyzed distances during the dry season. (b) Attraction from 6 - 12 m, and repulsion at 5, 11, and 14 m during the rainy season. Black solid line represent the Ripleys K bivariate pattern; red dashed lines represent the 95% CI; blue solid line shows the null hypothesis.

Fig. 1

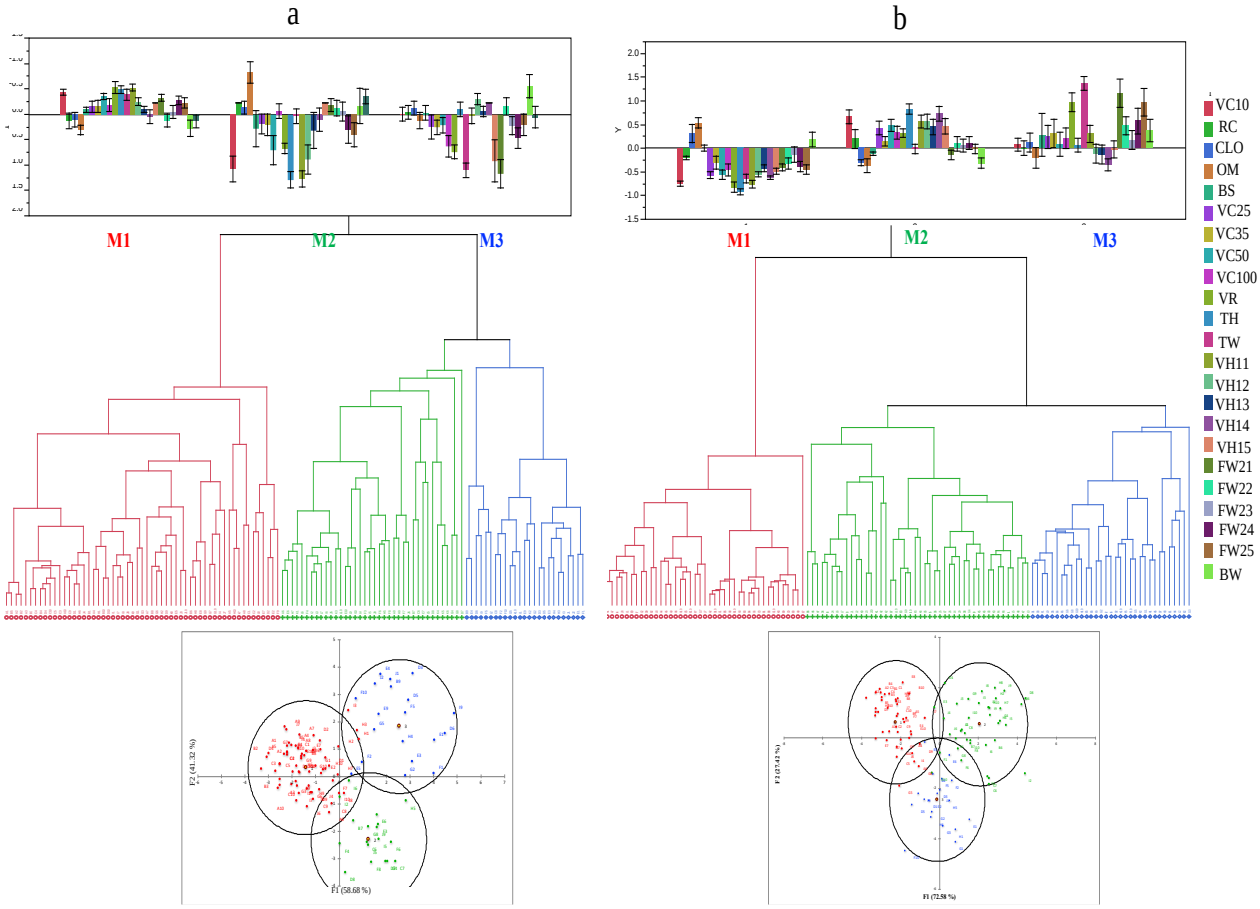

a
b
M1
M2
M3
M1
M2
M3
VC10
RC
CLO
OM
BS
VC25
VC35
VC50
VC100
VR
TH
TW
VH11
VH12
VH13
VH14
VH15
FW21
FW22
FW23
FW24
FW25
BW

Fig. 2

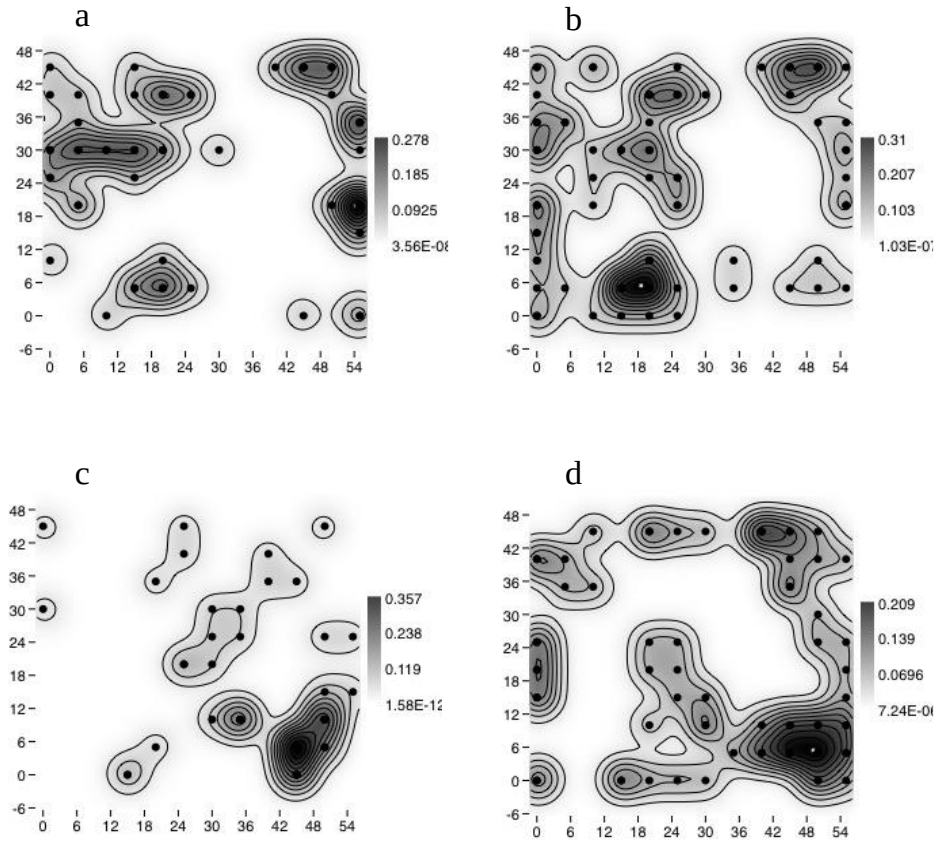
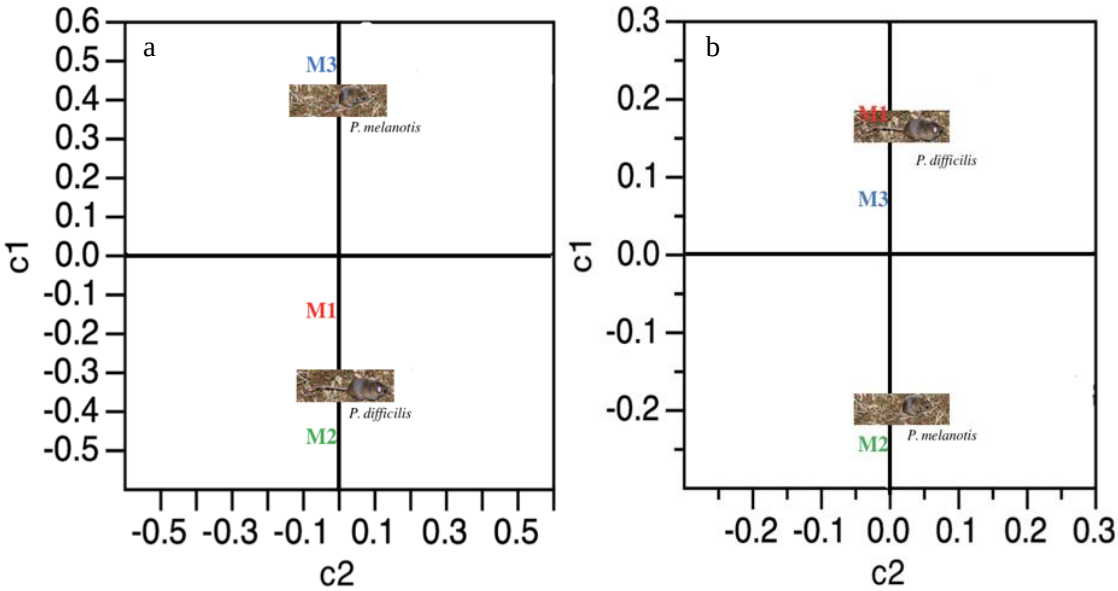

a
0.278
0.185
0.0925
3.56E-08
b
0.31
0.207
0.103
1.03E-07
c
0.357
0.238
0.119
1.58E-12
d
0.209
0.139
0.0696
7.24E-06

Fig. 3


a
M3
P. melanotis
M1
P. difficilis
M2
c1
c2
0.6
0.5
0.4
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.3
-0.4
-0.5
-0.5 -0.3 -0.1 0.1 0.3 0.5
b
M1
P. difficilis
M3
M2
P. melanotis
c1
c2
0.3
0.2
0.1
0.0
-0.1
-0.2
-0.2 -0.1 0.0 0.1 0.2 0.3

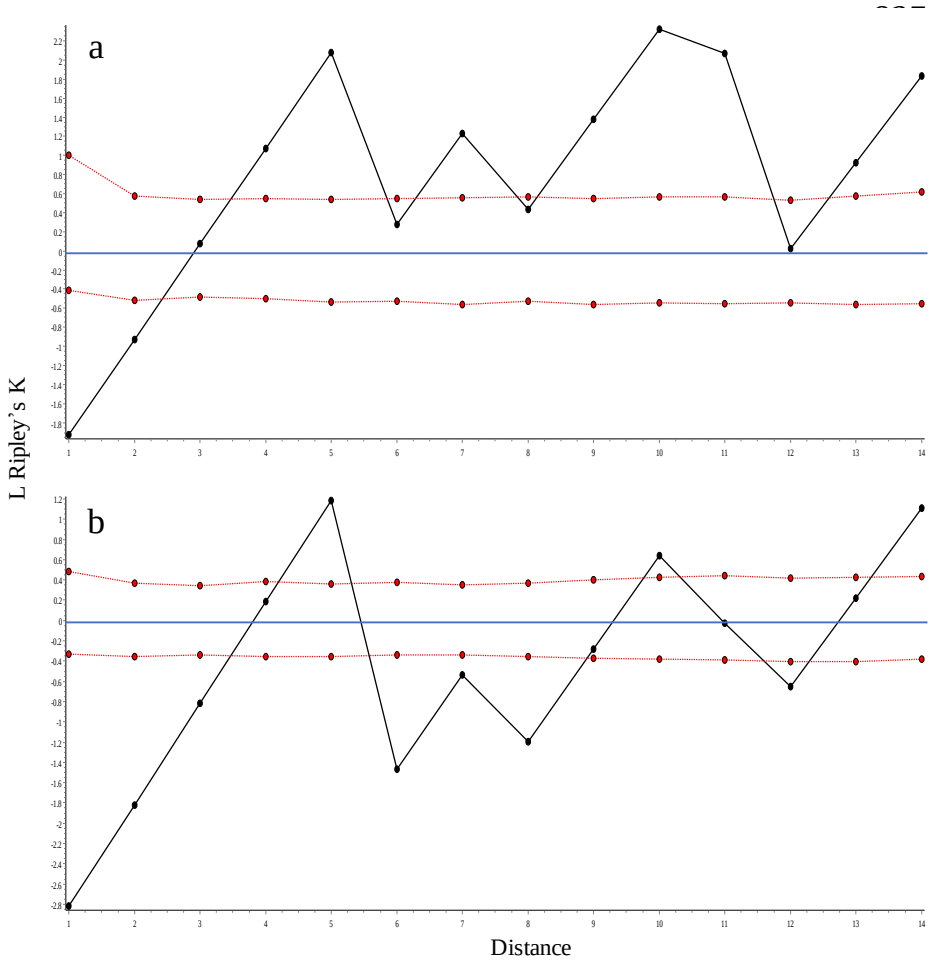



Fig. 4